

THE EXPANDING SCALE OF SPECIES TURNOVER EVENTS ON CORAL REEFS IN BELIZE

RICHARD B. ARONSON,^{1,2,5} IAN G. MACINTYRE,³ WILLIAM F. PRECHT,⁴ THADDEUS J. T. MURDOCH,^{1,2} AND CHERYL M. WAPNICK¹

¹Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, Alabama 36528 USA

²Department of Marine Sciences, University of South Alabama, Mobile, Alabama 36688 USA

³Department of Paleobiology, Smithsonian Institution, Washington, D.C. 20560 USA

⁴PBS&J, 2001 Northwest 107th Avenue, Miami, Florida 33172 USA

Abstract. Beginning in the late 1980s, white-band disease nearly eliminated the staghorn coral *Acropora cervicornis* from reefs in the central shelf lagoon of Belize. The lettuce coral *Agaricia tenuifolia* replaced *Acropora cervicornis* in the early 1990s, but anomalously high water temperatures in 1998 caused severe bleaching and catastrophic mortality of *Agaricia tenuifolia*. The short-lived transition in dominance from *Acropora cervicornis* to *Agaricia tenuifolia* left an unambiguous signature in the fossil record of these uncemented lagoonal reefs. Analysis of 38 cores, extracted from 22 sampling stations in a 375-km² area of the central lagoon, showed that *Acropora cervicornis* dominated continuously for at least 3000 years prior to the recent events. *Agaricia tenuifolia* occasionally grew in small patches, but no coral-to-coral replacement sequence occurred over the entire area until the late 1980s. Within a decade, the scale of species turnover increased from tens of square meters or less to hundreds of square kilometers or more. This unprecedented increase in the scale of turnover events is rooted in the accelerating pace of ecological change on coral reefs at the regional level.

Key words: Acropora; Agaricia; Belize; Caribbean; coral bleaching; coral disease; coral reef; Holocene; paleoecology; patch dynamics; species turnover; white-band disease.

INTRODUCTION

Coral reefs of the Caribbean region (the western Atlantic, including Florida and the Bahamas) have changed markedly since the late 1970s (Ginsburg 1994, Hughes 1994, McClanahan and Muthiga 1998). The essential features of this change are that (1) coral mortality from natural and, possibly, human causes has reduced coral cover and opened space on most reefs, (2) herbivory has been reduced by the 1983–1984 mass mortality of the sea urchin *Diadema antillarum* and, in at least some places, by overfishing of parrotfish (Scaridae) and surgeonfish (Acanthuridae), and (3) the increase in available space relative to the potential for herbivory has resulted in greatly increased cover and biomass of fleshy and filamentous macroalgae, especially forms that are unpalatable to herbivorous fishes (Knowlton 1992, Hughes 1994, Szmant 1997, Miller et al. 1999, Aronson and Precht 2000, 2001a, Williams and Polunin 2001). The increase in macroalgae has in turn limited coral recruitment and the recovery of coral populations, and has obscured zonation patterns that were formerly typical of Caribbean reefs (Jackson 1991, Edmunds and Carpenter 2001). If these recent decadal-scale changes are unique on a centennial to millennial scale, then the popular suspicion that hu-

mans are important agents of reef degradation could be well founded. Conversely, if changes of this sort occurred in the past, then human interference could be merely a minor factor contributing to the present situation.

Until the late 1970s, three framework-building coral species displayed a zonation pattern that was common throughout the region (Goreau 1959, Goreau and Goreau 1973, Graus and Macintyre 1989). Thickly branching elkhorn coral, *Acropora palmata*, dominated substratum cover from the reef crest down to 5 m depth on the fore reef under all but the most energetic wave conditions. The more thinly branching staghorn coral, *Acropora cervicornis*, dominated intermediate depths (5–25 m) on wave-exposed fore reefs. *Acropora cervicornis* ranged into shallower habitats on protected fore reefs and also occurred in back-reef and lagoonal habitats (Geister 1977, Rützler and Macintyre 1982, Hubbard 1988). The third primary framework builder of Caribbean reefs, the *Montastraea annularis* species complex, consists of at least three sibling species (Knowlton et al. 1992). Massive colonies of *Montastraea* spp. were (and remain) common in a variety of reef habitats, exhibiting interspecific zonation as well as intraspecific changes in morphology along depth gradients (Goreau 1959, Graus and Macintyre 1982, Knowlton et al. 1992).

The overall zonation pattern has largely disappeared because the *Acropora* spp. have been killed and re-

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⁵ E-mail: raronson@disl.org

placed by macroalgal species on most Caribbean reefs (Jackson 1991, Hughes 1994). A major cause of this regional-scale turnover has been white-band disease, a bacterial disease (or group of diseases) that affects only the genus *Acropora* (Rogers 1985, Santavy and Peters 1997, Richardson 1998, Bythell et al. 2000, Aronson and Precht 2001a, b). Hurricanes have also killed populations of *Acropora* spp., but mortality from hurricanes passing through particular areas has been localized to reefs in and near the storm tracks (Woodley et al. 1981, Woodley 1992). Furthermore, a number of areas within the Caribbean are rarely affected by cyclonic activity (Neumann et al. 1987, Treml et al. 1997). Other sources of local mortality of *Acropora* include cold water stress in Florida and the Bahamas (Porter et al. 1982, Roberts et al. 1982, Burns 1985, Jaap and Sargent 1994), coral bleaching associated with high temperatures (Cortés 1994), sediment and nutrient input (Weiss and Goddard 1977, Lewis 1984), and predation by corallivorous fish and invertebrates (Antonius 1977, Knowlton et al. 1990, Bruckner et al. 1997).

Pleistocene reefs around the Caribbean display fossilized patterns of coral zonation similar to those observed on modern reefs prior to the late 1970s (Meso-lella 1967, Boss and Liddell 1987, Jackson 1992, Greenstein et al. 1998, Pandolfi and Jackson 2001). Despite large fluctuations in sea level during the Pleistocene, the composition of Caribbean coral assemblages remained stable and predictable within habitats on a time scale of tens of thousands to hundreds of thousands of years. When viewed at finer spatial and temporal scales, however, the within-habitat composition of Pleistocene coral assemblages displays high variability (Jackson et al. 1996, Pandolfi 1996, Pandolfi and Jackson 1997). The transition to the present macroalgal-dominated state of Caribbean reefs, observed on a scale of decades, could be an aspect or a consequence of this short-term variability (Woodley 1992). On the other hand, the coral-to-algal transition could represent a rare or even unprecedented departure from the previous community composition, brought about by a unique conjunction of circumstances (Jackson 1991, 1994, Knowlton 1992, Hughes 1994).

Implicit in the latter alternative is a hypothesis about the scale of species turnover. If the current state of Caribbean reefs is unique, then the spatial scale of turnover events must have increased greatly, from localized areas of coral mortality and species replacement before the late 1970s to recent changes in biotic composition that transcend reefs and even reef systems. The most direct way to test this hypothesis is to examine the fossil record of reefs during the late Holocene (the last 3000 yr) on an intermediate temporal scale of hundreds to thousands of years.

Cores from the reef at Buck Island, St. Croix, (7000 yr BP to the 1970s) displayed an uninterrupted accumulation of well-preserved *Acropora palmata*, suggesting continuous reef growth and supporting the hy-

pothesis that the current situation is unusual (Hubbard et al. 1994). Likewise, cores extracted from Channel Cay, a lagoonal reef in central Belize, showed that *Acropora cervicornis* dominated that reef for at least the last several millennia, until it was killed by white-band disease after 1986 (Aronson and Precht 1997). The lettuce coral *Agaricia tenuifolia* then increased opportunistically and became the dominant space occupant. Although they are suggestive, these two studies were limited to small areas and did not explicitly test hypotheses about the changing scale of species turnover.

In this paper we expand Aronson and Precht's (1997) study in the Belizean shelf lagoon. We report the results of an intensive coring program carried out over a 375-km² area at two hierarchical levels (and two corresponding spatial scales): within sampling stations (meters to tens of meters) and among stations (hundreds of meters to kilometers). Although transitions from *Acropora cervicornis* to *Agaricia tenuifolia* occurred previously during the late Holocene, they were confined to small patches on reefs over distances of meters to tens of meters. Only recently did a transition to dominance by *Agaricia tenuifolia* take place over the entire area. Our findings reveal an orders-of-magnitude increase in the spatial extent of species turnover, which was unprecedented on a time scale of centuries to millennia.

STUDY AREA

Geological setting

The central sector of the Belizean shelf lagoon is characterized by diamond-shaped reefs known as rhomboid shoals (Fig. 1). These reefs reach sea level and surround sediment-filled basins that can be as deep as 30 m (Macintyre and Aronson 1997, Macintyre et al. 2000). The Holocene deposits on the rhomboid shoals, which are up to 20 m thick, accumulated over the past 8000–9000 yr (Westphall and Ginsburg 1984, Precht 1993), and they lie directly atop bathymetric highs composed of Pleistocene reef limestones (e.g., Halley et al. 1977). The cause of the atoll-like configuration has been debated but structural control appears to be of primary importance, with the original reef growth occurring around the edges of fault blocks (Purdy 1974a, b, Lara 1993, Precht 1997, Esker et al. 1998; but see Ferro et al. 1999). Subsequent accretion followed and exaggerated the antecedent topography, resulting in reef slopes that can be quite steep (Westphall 1986, Macintyre et al. 2000).

The energy of waves impinging on the central lagoon is attenuated by the continuous barrier reef to the east (seaward) and by Glovers Reef, an atoll-like carbonate platform east of the barrier reef (Burke 1982). Because the rhomboid shoals are situated in a low-energy environment, there is little or no submarine cementation of the reefs (see Purser and Schroeder 1986, Macintyre

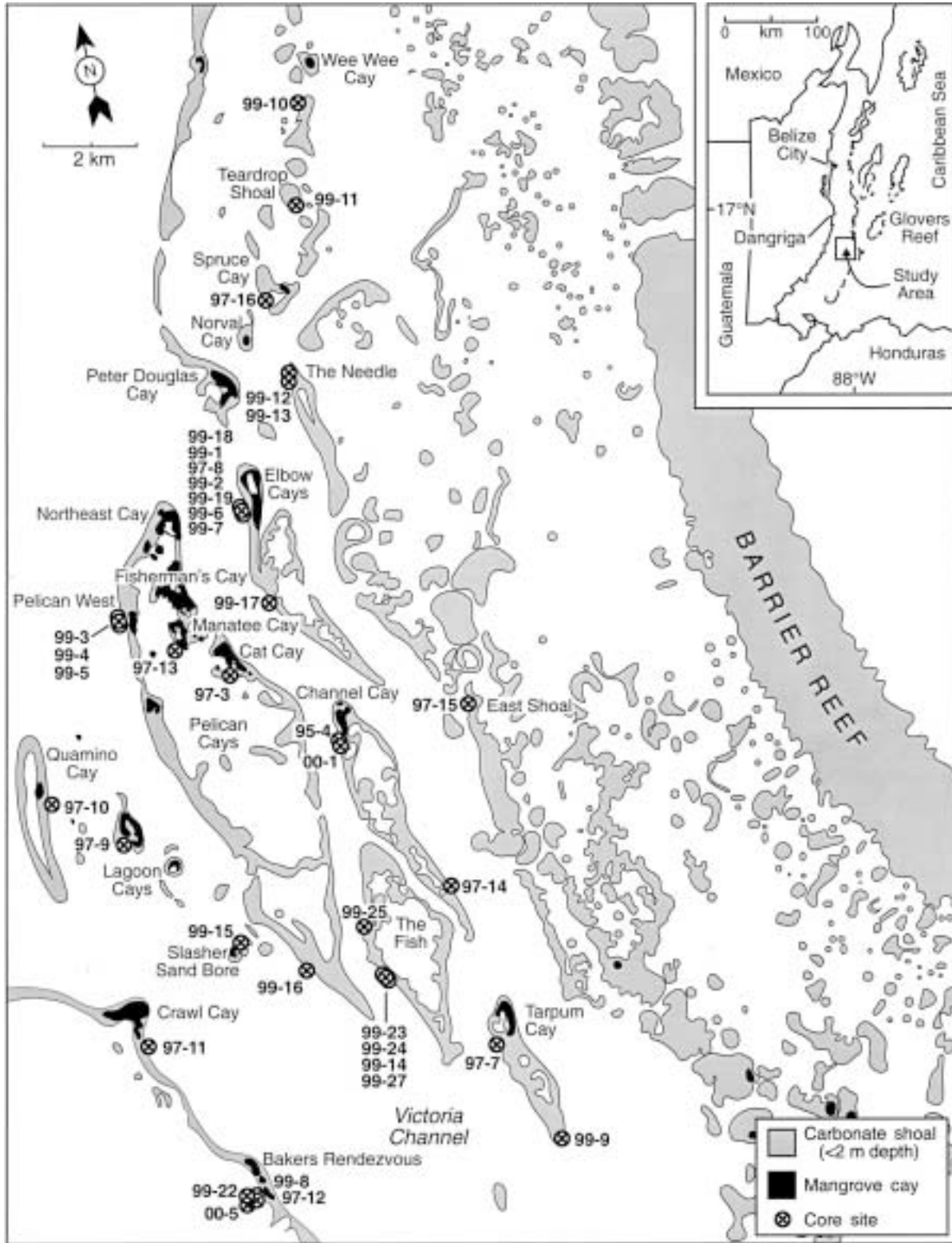


FIG. 1. Map of the central shelf lagoon of the Belizean Barrier Reef, showing the rhomboid shoals and coring stations. Each station is a length of reef, meters to several tens of meters long, within which one or more cores were extracted. The map is based on a Landsat 5 TM image (18 September 1987) supplied by G. Madejski, NASA Goddard Space Institute, Greenbelt, Maryland, USA.

and Marshall 1988). Living and dead coral colonies are stabilized on the reef slopes by the interlocking of their skeletons. Debris fans at the bases of the rhomboid shoals (22–30 m water depth) suggest occasional storm disturbance; however, Hurricanes Greta (September 1978), Mitch (October 1998), Keith (October 2000), and Iris (October 2001; a Category 4 storm and nearly a direct hit) did not appreciably affect the layering of Holocene sediments as reported in this paper (Westphall 1986, Aronson et al. 2000; R. Aronson and W. Precht, unpublished data).

The Holocene deposits at Channel Cay, the best-studied of the rhomboid shoals, are composed primarily of an open framework of interlocking branches of *Acropora cervicornis* (Shinn et al. 1979, Westphall 1986, Aronson and Precht 1997, Aronson et al. 1998). Coring operations and observations of submarine exposures in the present study revealed the same Holocene architecture on the other rhomboid shoals. The steep slopes of 45° or more observed in some areas along the outer flanks of the shoals were created by the rapid growth of *Acropora cervicornis* as the reefs caught up to sea level (Westphall 1986, Macintyre et al. 2000).

Recent ecological changes

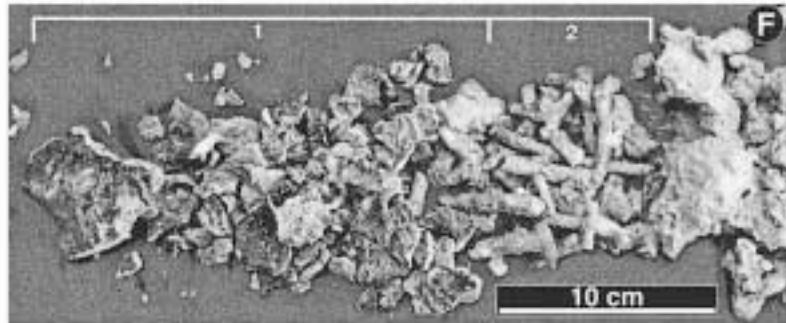
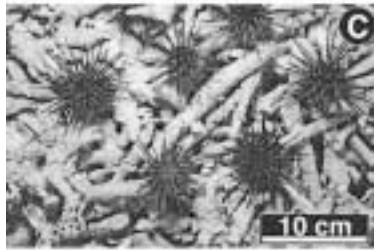
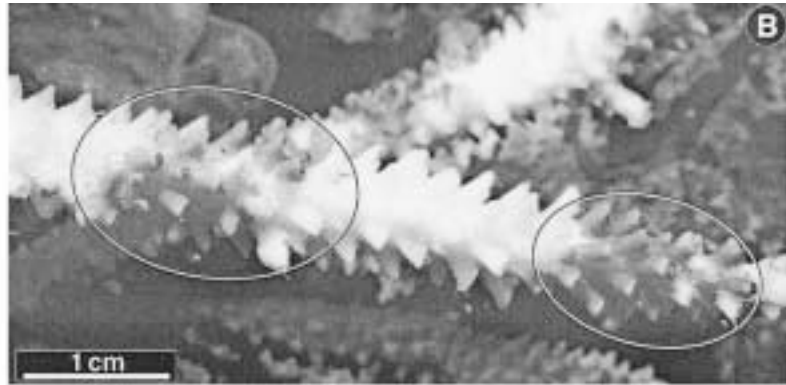
Before the late 1980s, the outer flanks of the rhomboid shoals were covered by living populations of *Acropora cervicornis* (>70% cover in some places; Fig. 2A) from 2–15 m depth (Shinn et al. 1979, Westphall 1986, Aronson and Precht 1997). *Agaricia tenuifolia* and other coral species in the family Agariciidae were subdominant components in that depth range, and they dominated the benthos below 15 m. The most common corals in the shallowest depths (≤ 1 m) were the finger coral *Porites divaricata* and the hydrozoan fire coral *Millepora alcicornis* (Aronson et al. 1998, Macintyre et al. 2000). During the 1980s, white-band disease (WBD; Fig. 2B) nearly eliminated the *Acropora cervicornis* populations on the rhomboid shoals.

Acropora cervicornis colonies killed by WBD collapsed rapidly due to the weakening effects of bioer-

rosion. Fleshy and filamentous macroalgae that colonized the coral skeletons were consumed by the echinoid *Echinometra viridis* (Fig. 2C). *Agaricia tenuifolia* and the other agariciids readily recruited to and grew on the *Echinometra*-grazed *Acropora cervicornis* rubble (cf. Sammarco's [1982] experiments in Jamaica, in which grazing by *E. viridis* promoted the recruitment of agariciids). The cover of *Agaricia tenuifolia* then increased dramatically (Fig. 2D), reaching levels as high as 85% (Aronson et al. 2000). Colonies of *Agaricia tenuifolia* growing in this lagoonal setting formed assemblies of vertical blades with an overall inverted-pyramid shape. As they grew tall (>0.5–1 m height), their high center of gravity eventually caused them to topple over, leaving small scree slopes of *Agaricia* rubble. Although large amounts of coral rubble were available for settlement, herbivory by *E. viridis* kept the rubble free of algal growth (<10% cover), permitting *Agaricia tenuifolia* to continue recruiting at a high rate (Edmunds et al. 1998). The cover of 18 or more other coral species remained low ($\leq 9\%$) from 1986 to 2000 (Aronson and Precht 1997, Aronson et al. 2000). This *Acropora*-to-*Agaricia* transition occurred throughout the central and southern shelf lagoon over an area of at least 500 km².

The upward growth of interlocking *Acropora cervicornis* colonies produced the slopes that characterized the flanks of the rhomboid shoals, as described in the previous section. In contrast, *Agaricia tenuifolia* was uncommon on steep slopes. We determined that the maximum angle of repose for *Agaricia tenuifolia* was $\sim 45^\circ$, based on (1) the cover of live *Agaricia tenuifolia* in 1996, and (2) measurements of the accretion of *Agaricia tenuifolia* (thickness of accumulation of *Agaricia tenuifolia* rubble) over the period 1986–1996 on slopes of varying steepness. Slopes of 35–45° had reduced quantities of living *Agaricia tenuifolia* and *Agaricia tenuifolia* rubble. Slopes >45° were generally barren of *Agaricia tenuifolia* and were characterized by dead interlocking branches of *Acropora cervicornis* protruding from the reef flanks. Living and dead col-

FIG. 2. Photographs from the rhomboid shoals in Belize. (A) Stand of *Acropora cervicornis*, the species that dominated at 2–15 m water depth until the late 1980s. (B) Closeup of a branch of *Acropora cervicornis* infected with white-band disease. The diseased, white segments along the branch in the foreground, left and center, are characterized by dead skeleton and sloughing tissue. The darker segments, enclosed in ellipses, contain polyps that are beginning to show signs of the disease. (C) *Echinometra viridis* grazing on rubble of *Acropora cervicornis* killed by white-band disease. Note the complete removal of surface sculpture from the branch fragments. (D) *Agaricia tenuifolia* dominant at Cat Cay in June 1994, 5 m depth. Note *Acropora cervicornis* colonies on the left. The *Agaricia tenuifolia* was killed by high water temperatures in 1998. (E) Divers positioning a 5-m core tube. Tubes were driven into the reef framework with the aid of adjustable core slips, visible in the foreground below the diver's arms. (F) Top portion of a core from Channel Cay, showing (1) uppermost layer of *Agaricia tenuifolia* plates, and (2) layer of degraded branch fragments of *Acropora cervicornis* just below uppermost layer. Coral rubble at the extreme right of the photograph (lower in the core) is packed in muddy sediment. The layers in the pictured core were especially obvious, but they were discrete and easily identifiable in the other cores as well. (G) Eroded branch fragments of *Acropora cervicornis* from just below the uppermost *Agaricia tenuifolia* layer in core 97-12, encrusted with *Agaricia* recruits. (H) Segment of a core from the Pelican Cays, spanning (left to right) 40–65 cm below the top. The dominant constituents are lightly altered branch fragments of *Acropora cervicornis*. The sand- and mud-sized sediments have been washed away.



onies of *Agaricia tenuifolia* were too top-heavy and accumulations of imbricated *Agaricia tenuifolia* plates were too unstable to persist on these steep slopes.

Agaricia tenuifolia dominated benthic cover on the rhomboid shoals in the 3- to 15-m depth range from the early 1990s until 1998. Abnormally high water temperatures in the summer and fall of 1998 caused almost all coral colonies in the central lagoon to expel their zooxanthellae and bleach. By January 1999, the *Agaricia tenuifolia* had died catastrophically, dropping to near-zero cover (Aronson et al. 2000). A few small colonies survived in deeper water (>15 m), but there were no signs of recovery as late as March 2001.

METHODS

Coring operations

In order to reconstruct the ecological history of the rhomboid shoals during the late Holocene, 38 push cores were extracted by hand from the study area (Fig. 1). In this diver-operated, open-barrel, coring technique, a 4- to 5-m segment of 7.6 cm (3 inch) diameter aluminum tubing was forced into the reef (Fig. 2E). While one diver held the top of the core tube to maintain its vertical orientation, two others worked the tube into the reef using adjustable core slips with handles. Once the tube had been driven in ~1 m, the first diver sleeved a sliding hammer weight over the top of the tube and tapped the tube to aid penetration. Teeth on the bottom of the core tube also enhanced penetration, by cutting through branching and massive coral skeletons (Dardeau et al. 2000).

The tube was generally driven 3–4 m into the sediment, leaving 0.5–1 m extending above the sediment–water interface. At that point, penetration was calculated by measuring the final length of the exposed portion of the tube and subtracting that from the total length of the tube. Recovery was estimated in situ by feeding a weighted fiberglass surveyor's tape into the core tube until it reached the top of the recovered sediment; the estimated recovery was calculated as the difference between the length of the tube and the length of the empty (water-filled) portion of the tube. After these measurements were made, the exposed (top) end was capped and then sealed with electrical tape. The core was pulled from the reef by hand and the bottom was capped and taped. It was carried to the water surface, loaded onto a boat, and taken to the Smithsonian Institution's field station at Carrie Bow Cay. For some cores, penetration was measured and recovery estimated in situ at intervals during the coring operation to ascertain whether material was entering the core tube continuously or instead binding and preventing further recovery.

The cores were extracted from water depths of 4.2–9.0 m, with the exception of four cores taken from depths 9.6–11.5 m (Table 1). Considering the depths of penetration of the cores and the position of sea level

over the past 3000 yr, the cores sampled the reefs at paleodepths <15 m. The 15-m limit is the depth below which agariciids predominated before the recent *Acropora* kill, according to ecological observations (Aronson and Precht 1997); coring paleodepths below 15 m would not have been relevant to testing hypotheses about transitions from *Acropora cervicornis* to *Agaricia tenuifolia*, because *Acropora cervicornis* may never have dominated at those depths.

Contemporary slopes and paleoslopes >45° should be biased against the preservation of *Agaricia tenuifolia* layers but not against the preservation of *Acropora cervicornis*. Westphall (1986) showed from patterns of vertical accretion and horizontal progradation at Channel Cay that paleoslope angles are necessarily lower than the overlying modern slope angles, and Macintyre et al. (2000) obtained similar results for the Pelican Cays (Fig. 1). To eliminate any bias introduced by slope angle, we extracted cores only from areas in which the contemporary slope angles, and therefore the paleoslope angles, were less than the critical angle of 45°. For each core, the contemporary slope angle was measured underwater with a hand-held inclinometer, and almost all were <35° (Table 1).

Laboratory analysis

Each core was extruded in the laboratory. Samples of the interstitial sediment were collected for analysis, and the remaining sand-sized and smaller fractions were washed away. The core was logged in 5-cm intervals. The relative abundances of coral species were assessed visually and recorded for each interval, along with their taphonomic states and spatial orientations. Most of the coral material was *Acropora cervicornis* and *Agaricia tenuifolia*. The calcareous remains of other invertebrates and algae were also noted. A detailed column diagram was made of the core, and a coral sample was collected from the base of each core for radiocarbon dating.

The taphonomic state of *Acropora cervicornis* was categorized as either lightly altered or degraded. Lightly altered branch fragments retained most or all of their surface sculpture and were not heavily encrusted or bored (taphonomic categories 1 and 2 established for *Acropora cervicornis* by Greenstein and Moffat [1996]). Degraded branch fragments were eroded to the point that they retained little or none of their original surface sculpture, and they were encrusted and/or bored (categories 3–5 of Greenstein and Moffat [1996]). The same criteria were applied to plates of *Agaricia tenuifolia*.

A coral species in a particular taphonomic state was considered dominant if it constituted >50% of the skeletal fragments in the interval, but in practice the dominants often constituted 70% or more of the material. Subdominant categories were those that constituted 10–50%, and rare categories constituted <10%. Quantitative analysis of the cores, beyond placing the con-

TABLE 1. Data on cores from the rhomboid shoals, presented in chronological order of extraction.

Core	Location	Slope angle (°)	Water depth (m)	Penetration (cm)	Recovery (cm)	¹⁴ C age (yr ± SE)
95-4	Channel Cay North	21	6.1	428	267	3130 ± 100
97-3	Cat Cay	18	7.8	339	145	500 ± 70
97-7	Tarpum Cay North	32	9.0	315	100	880 ± 60
97-8	Elbow Cays	10	5.1	347	200	1500 ± 40
97-9	Lagoon Cays	25	5.4	347	150	730 ± 70
97-10	Quamino Cay	26	5.4	337	140	1280 ± 70
97-11	Crawl Cay	4	8.7	332	200	2670 ± 70
97-12	Bakers Rendezvous	12	4.5	344	145	470 ± 60
97-13	Manatee Cay	10	5.7	226	90	520 ± 60
97-14	Channel Cay South	11	6.0	317	145	970 ± 70
97-15	East Shoal	30	4.2	179	45	640 ± 60
97-16	Spruce Cay	19	5.4	341	75	2220 ± 60
99-1	Elbow Cays	22	6.0	405	210	310 ± 60
99-2	Elbow Cays	30	11.5	400	110	510 ± 60
99-3	Pelican West	16	6.0	384	110	1210 ± 60
99-4	Pelican West	16	6.0	370	65	940 ± 60
99-5	Pelican West	34	9.6	407	80	1140 ± 70
99-6	Elbow Cays	29	9.0	391	85	330 ± 40
99-7	Elbow Cays	29	9.0	414	115	440 ± 70
99-8	Bakers Rendezvous	10	6.6	405	150	170 ± 60
99-9	Tarpum Cay South	36	6.6	165	75	1470 ± 60
99-10	Wee Wee Cay	30	4.8	400	110	1340 ± 60
99-11	Teardrop Shoal	10	7.5	292	72	1290 ± 60
99-12	The Needle	28	7.2	270	85	1250 ± 70
99-13	The Needle	32	7.2	400	150	2060 ± 70
99-14	The Fish	20	10.0	375	170	470 ± 70
99-15	Slasher Sand Bore	38	6.6	403	204	610 ± 60
99-16	Pelican South	20	6.3	338	90	630 ± 60
99-17	Elbow Cays	24	6.6	266	100	280 ± 60
99-18	Elbow Cays	18	7.2	380	115	490 ± 60
99-19	Elbow Cays	17	7.5	400	115	350 ± 60
99-22	Bakers Rendezvous	31	6.3	400	100	270 ± 60
99-23	The Fish	28	10.8	290	100	620 ± 60
99-24	The Fish	18	7.2	410	210	730 ± 60
99-25	The Fish	15	5.1	375	215	1040 ± 50
99-27	The Fish	26	8.7	341	120	3480 ± 70
00-1	Channel Cay North	28	9.0	394	105	1670 ± 70
00-5	Bakers Rendezvous	8	6.0	375	120	250 ± 60

Notes: The year in which each core was extracted is indicated by the number 95, 97, 99, or 00. Ages are reported as uncorrected radiocarbon years before 1950 ± 1 SE for coral samples taken from the bottoms of the cores. All dates are based on standard radiometric dating except the date for core 97-8, which was obtained from a small coral sample using absorption mass spectroscopy (AMS). Core 95-4 is from Aronson et al. (1998).

stituents in these ranked categories, was not necessary. In another study, the ranked-category approach was compared to two analyses of a more quantitative nature. Fifteen push cores were extracted from similar, un cemented, lagoonal reefs in the Bahía Almirante, near Bocas del Toro, northwestern Panamá. These cores were assessed visually as described above, but in addition the constituents of each 5-cm interval were quantified by both weight and volume. Core logs based on weights and volumes were essentially identical to core logs based on visual assessments, validating the non-parametric ranking approach employed in the present study.

The dominant constituents of most of the core intervals were lightly altered (or unaltered) branch fragments of *Acropora cervicornis*. Some cores contained

subsurface layers of plates of *Agaricia tenuifolia*, indicating species turnover on a local or possibly larger scale. Other cores contained subsurface layers of heavily eroded *Acropora cervicornis* rubble encrusted with juvenile colonies of *Agaricia* spp. and other coral species; these layers of degraded material indicated mortality of *Acropora cervicornis* and exposure of the dead skeletons at the sediment-water interface, but incomplete species replacement. Both types of layers were discrete and plainly obvious from visual examination of the cores and from the core logs. A sample was collected from the base of each of these layers for radiocarbon dating.

Radiometric age determinations were performed using standard techniques by Beta Analytic, Inc. (Miami, Florida, USA). Dates are reported as uncorrected ra-

diocarbon years before 1950, using a Libby half-life of 5568 yr and a modern standard based on 95% of the activity of the National Bureau of Standards' oxalic acid. Uncorrected dates are used so that they may be compared with published sea-level curves; most sea-level curves for Belize and elsewhere in the Caribbean are based on uncorrected dates (Lighty et al. 1982, Macintyre et al. 1995). Correcting for the DeVries effect, the reservoir effect, and natural isotopic fractionation yielded calibrated dates that were generally within a few decades of the uncorrected dates. The uncorrected dates, therefore, provide reasonable approximations of the corresponding ages in calendar years before present. Whether the radiocarbon dates are corrected or not has no bearing on the tests of hypotheses.

Sampling design

The coring program was carried out at two spatial scales. There were 22 coring stations spread over the central lagoon, with the locations chosen to maximize the area sampled. We extracted multiple cores from six of these stations. The intensively sampled stations included Elbow Cays, The Fish, and Bakers Rendezvous, because a core from each of these stations contained a layer suggesting complete or incomplete *Acropora*-to-*Agaricia* turnover at an age of 270–380 radiocarbon years. The two-tiered sampling design made it possible to determine whether such layers in particular cores represented events that had occurred over shorter distances within stations (meters to tens of meters) or over longer distances among stations (hundreds of meters to kilometers).

In a number of cases more than one station was sampled on a single rhomboid shoal. Given the known dispersal abilities of coral larvae (Harrison and Wallace 1990, Edinger and Risk 1995, Richmond 1997) and the regional nature of WBD outbreaks, there was no reason to expect that stations on the same shoal would be more similar to each other than to stations on other shoals, which in many cases were closer. For the purpose of this analysis, the stations were treated as replicates at the scale of the study area.

Taphonomic and methodological considerations

Hubbard et al. (1994) reported low preservation potential of *Agaricia* spp. in fore-reef environments, possibly due to taphonomic alteration prior to burial. In contrast, Aronson and Precht (1997) observed that *Agaricia tenuifolia* had a high preservation potential in the subsurface sediments of the rhomboid shoals. Furthermore, push cores extracted from the Bahía Almirante in Panamá contained large quantities of *Agaricia tenuifolia* in various preservational states, as well as branching *Porites* spp. and *Acropora cervicornis*. There did not appear to be a taphonomic bias against *Agaricia tenuifolia* in that case either.

The coring procedure used in this study has distinct advantages over other techniques, such as piston cor-

ing, percussion coring, and vibracoring. Although other methods allow greater penetrations and can yield greater recoveries, they require complex logistics, including more divers, more hardware, and surface support. The open-barrel push-coring method is simple, quick, portable, and relatively inexpensive, enabling us to obtain records of sufficiently long time intervals with sample sizes sufficiently large for statistical analysis (Dardeau et al. 2000).

RESULTS

Species dominance and turnover

Thirty-eight cores were recovered from 22 sampling stations in the central sector of the shelf lagoon of the Belizean Barrier Reef (Fig. 1). The cores penetrated several meters into the uncemented reef framework. Radiocarbon analysis yielded a maximum uncorrected ^{14}C date of >3000 yr (Table 1).

All 38 cores contained an uppermost layer of imbricated, lightly altered *Agaricia tenuifolia* plates overlying a thick accumulation of *Acropora cervicornis* branches (Figs. 2E, 3). This *Agaricia tenuifolia* layer was ~0.25 m thick in most of the cores. From the lower half of the uppermost *Agaricia tenuifolia* layer down to the bottom of each core, the coral skeletons were surrounded by a matrix of sandy carbonate mud; only the upper half of the uppermost *Agaricia tenuifolia* layer was free of matrix (see also Aronson and Precht 1997). There was no evidence of bioturbation or other large-scale reworking of the sandy-mud matrix.

In all the cores, the length of the recovered material was shorter than the depth of penetration into the reef (Table 1). The actual recoveries, measured as the lengths of the extruded material, differed little from the in situ estimates of recovery, indicating little or no loss from the bottoms of the core tubes during removal from the reef. The measurements of penetration and the in situ estimates of recovery made at intervals during some of the coring operations indicated that material entered the core tubes continuously as they were forced into the reef. This means that the differences between penetration and recovery were due to compaction; sediment did not bind in the tubes and prevent further recovery. There was no indication that the low recoveries were due to voids in the reef framework; there were no sudden periods of rapid penetration, nor were there any suggestions of empty spaces from the measurements of recovery during the procedure.

A thin layer of eroded and encrusted *Acropora cervicornis* rubble lay just beneath the uppermost *Agaricia tenuifolia* layer, with the branch fragments in a horizontal orientation (Fig. 2F, G). This layer of degraded *Acropora cervicornis* rubble recorded the mass mortality of the populations from WBD. Post-mortem exposure of the skeletal branches at the sediment–water interface allowed extensive abrasion by grazing echinoids prior to burial, to the extent that almost none of

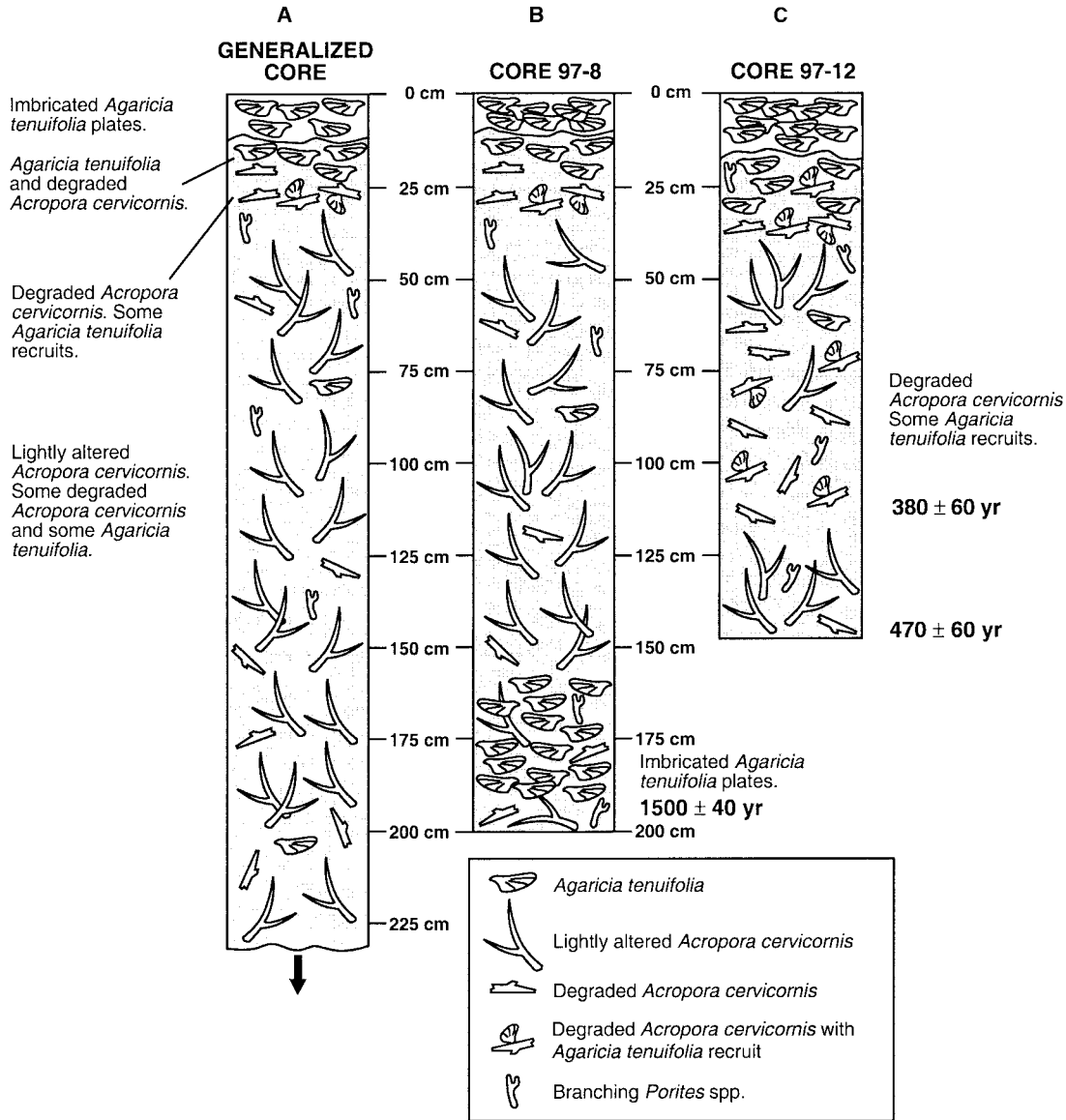


FIG. 3. Representative cores. Gray fill represents sandy mud, and wavy horizontal lines demarcate the upper limit of sandy-mud sediment. (A) Composite diagram based on the majority of core logs. The uppermost layers of imbricated *Agaricia tenuifolia* plates and eroded, encrusted *Acropora cervicornis* rubble were deposited in the 1980s–1990s. (B) Log of core 97-8 from Elbow Cay, showing a 1500-yr-old layer of plates of *Agaricia tenuifolia*. (C) Log of core 97-12 from Bakers Rendezvous, showing a 380-yr-old layer in *Acropora cervicornis* rubble that was heavily eroded and encrusted with small colonies of *Agaricia tenuifolia*.

the original surface sculpture remained (see Greenstein and Moffat 1996). Encrustation of the eroded *Acropora cervicornis* rubble resulted from the recruitment and growth of *Agaricia tenuifolia*, other agariciids, other coral species, and occasionally crustose coralline algae (Fig. 2G; Aronson and Precht 1997).

Below the layer of degraded *Acropora cervicornis*, the subsurface Holocene was dominated by unaltered to lightly altered branches of *Acropora cervicornis*. These branches were generally unencrusted and un-bored, and they retained much of their original sculp-

ture (Figs. 2H, 3A). Many of these fresh-looking branches were oriented at positive angles from the horizontal, suggesting that for >3000 yr *Acropora cervicornis* colonies grew rapidly on top of the dead skeletons of their conspecific predecessors. Rapid growth and rapid burial were also reflected as accumulations of lightly altered coral branches oriented in growth or near-growth position in trenches dug into the reef flanks (Aronson and Precht 1997) and in natural exposures of *Acropora cervicornis* branches observed on steep slopes.

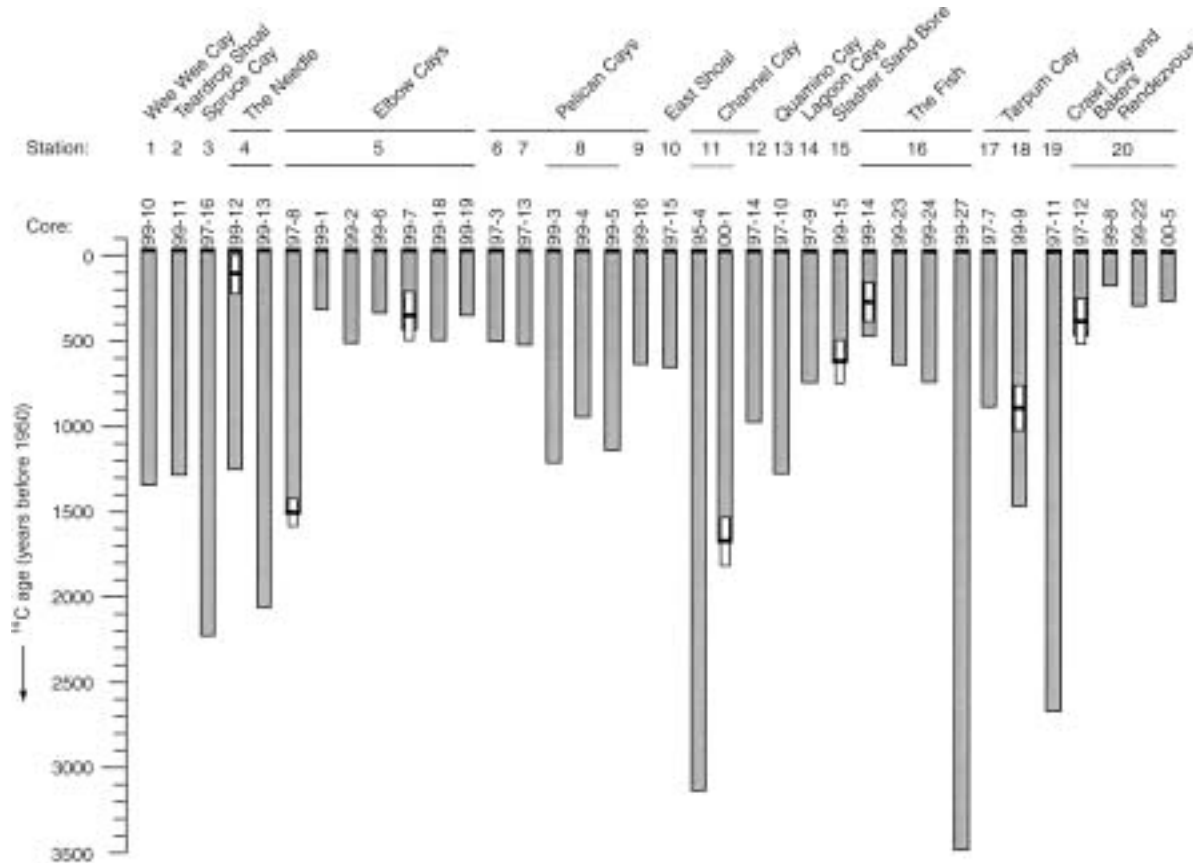


FIG. 4. Radiocarbon ages of the cores. The cores are grouped by station and shoal, and the shoals are arranged roughly from north to south. The coring stations are shown in Fig. 1. Gray fill represents ecological dominance by *Acropora cervicornis*, and horizontal black bars mark departures from the *Acropora*-dominated state. The black bars at the tops denote the recent mortality of *Acropora cervicornis* and the transition to *Agaricia tenuifolia*, visible in all cores. Other black bars mark the complete and incomplete transitions to *Agaricia tenuifolia* reported in Table 2. The vertical white bars represent the 95% confidence intervals of the radiocarbon dates of these anomalous layers, calculated as ± 1.96 SE. For clarity of presentation, confidence intervals are omitted from the dates of the bottoms of the cores, except where the bottom of an anomalous layer is also the bottom of a core.

The highly ordered layering pattern of well-preserved, fragile corals in all but two of the 38 cores indicated that the corals were buried and preserved in place with minimal transport. In other words, the core samples were composed primarily of autochthonous material, which reflected the constituents of the living communities at various times (Greenstein and Pandolfi 1997). Two cores, 99-17 from Elbow Cays and 99-25 from The Fish, contained more homogeneous, less structured accumulations of degraded *Acropora cervicornis* mixed with small amounts of *Agaricia tenuifolia* rubble. The mixed nature of these death assemblages suggested allochthonous sources. The presence in core 99-25 of large quantities of *Porites divaricata*, a coral from much shallower water (see *Study Area*), also suggested allochthonous input. These two cores are interpreted as coming from leeward drapes of storm-transported material (cf. Logan 1969) or from downslope transport of slumped material, and they are not considered further. This leaves 36 cores from 20

sampling stations that can be used to reconstruct the late Holocene history of reefs of the central lagoon.

The massive corals *Colpophyllia natans*, *Porites astreoides*, and *Montastraea* spp., and several other species of scleractinians, appeared occasionally in the cores as they did in the living community. The cores showed no obvious evidence of area-wide replacement by and subsequent disappearance of *Agaricia tenuifolia* in the three millennia before the late 1980s. Nevertheless, five cores displayed distinct subsurface layers of lightly altered *Agaricia tenuifolia* plates (Fig. 3B). Three cores contained distinct layers of eroded *Acropora cervicornis* branch fragments, with some of the fragments encrusted by recruits of *Agaricia tenuifolia* and other coral species (Fig. 3C).

The geographic distribution of these "anomalous" layers suggests spatial isolation of the turnover and incomplete turnover events they represent, since none of the layers occurred more than once at a single sampling station or on a single shoal (Fig. 4). Furthermore,

TABLE 2. Records of anomalous layers in the cores.

Core	Location	Type of layer	¹⁴ C age
97-8	Elbow Cays	<i>Agaricia tenuifolia</i> plates	1,500 ± 40
97-12	Bakers Rendezvous	eroded <i>Acropora cervicornis</i> , recruits	380 ± 60
99-7	Elbow Cays	<i>Agaricia tenuifolia</i> plates	340 ± 70
99-9	Tarpum Cay	eroded <i>Acropora cervicornis</i> , recruits	890 ± 60
99-12	The Needle	eroded <i>Acropora cervicornis</i> , recruits	110 ± 60
99-14	The Fish	<i>Agaricia tenuifolia</i> plates	270 ± 60
99-15	Slasher Sand Bore	<i>Agaricia tenuifolia</i> plates	610 ± 60
00-1	Channel Cay	<i>Agaricia tenuifolia</i> plates	1,670 ± 70

Notes: Layers of *Agaricia tenuifolia* plates indicate *Acropora*-to-*Agaricia* transitions. Layers of eroded branches of *Acropora cervicornis* encrusted with *Agaricia tenuifolia* recruits indicate incomplete transitions. Dates are for coral samples from the bases of the layers.

five of the layers were temporally unique (Table 2). These five layers can be interpreted tentatively as recording occurrences over distances smaller than the distances between stations. An *Agaricia tenuifolia* layer could, in fact, represent the temporary establishment and growth of a single colony. In a similar vein, a layer of eroded *Acropora cervicornis* branches encrusted with *Agaricia* recruits could represent the death of a small patch on which *Agaricia tenuifolia* was not fully able to establish itself before growth of *Acropora cervicornis* from the periphery closed the patch.

The remaining three cores with anomalous layers are more difficult to reconcile with the idea that episodes of species turnover occurred only on small spatial scales. Core 97-12 from Bakers Rendezvous, core 99-7 from Elbow Cays, and core 99-14 from The Fish contained layers that suggest approximately contemporaneous interruptions in the growth of *Acropora cervicornis* dating to 270–380 radiocarbon years. In all three cases, the 95% confidence interval about the date of the layer, calculated as 1.96 SE, overlapped the dates of the anomalous layers in the other two cores (Fig. 4).

There are two simple, mutually exclusive explanations for these data. The first is the alternative hypothesis that the three cores contain the record of an event that occurred throughout the central lagoon, but that signal was lost from all the other cores through degradation, slumping, downslope transport, or other taphonomic processes occurring at the scale of the coring station or at smaller scales. It should be noted that area-wide episodes of downslope transport would have been unlikely, considering the low angles of the paleoslopes sampled and the low wave energy that characterized the lagoonal environment. Cores 99-17 and 99-25 suggest transport in at least some places, however.

The second explanation is that the three dates are coincidental. In this null hypothesis, the fossil record is taken at face value: prior to the late 1980s, complete and interrupted replacements of *Acropora cervicornis* by *Agaricia tenuifolia* occurred locally and independently. Binomial probability analysis can be used to test these hypotheses.

Probability analysis

Let us assume that cores 97-12, 99-7, and 99-14 contain evidence of a large-scale replacement event in the 200–400-yr range, which was not preserved in the other cores from those three stations, nor in the cores from any other stations. Let us further assume that the failures of preservation were due to taphonomic processes occurring at the scale of the coring station or at smaller scales. Working from these assumptions, we can first estimate the probability that such an event layer appearing in one core at a station will be lost from sediments sampled by other cores at the same station. We can then use the within-station failure estimate to calculate the probability that only three stations will show any evidence of the putative large-scale event.

Nine cores collected from the stations at Elbow Cays, The Fish, and Bakers Rendezvous had bottom dates that were ≥ 388 radiocarbon years (270 yr + 1.96 SE in core 99-14; Fig. 4). Only one of the four cores extracted from Bakers Rendezvous—the one containing the anomalous layer—is relevant to this analysis, because the material in the other three cores was too young to span the time interval of that anomalous layer (Table 1, Fig. 4). The cores from Bakers Rendezvous, therefore, cannot be used to calculate the within-station failure rate because there is no within-station replication at the radiocarbon age of interest. Eight cores from Elbow Cays and The Fish can be used, and two of these contain evidence of the alleged large-scale event. The estimated probability of an individual core failing to preserve evidence of a species turnover event suspected to have occurred at the scale of the coring station or at a larger scale is thus $(8-2)/8$, or 0.75.

Since 30 cores from 20 stations dated to ≥ 388 radiocarbon years, the mean number of cores per station for this analysis is 30/20, or 1.50. The average probability of no cores from a given station recording a large-scale turnover event is $q = 0.75^{1.50} = 0.6495$. The probability of at least one core from that station recording the event is $p = 1.0000 - 0.6495 = 0.3505$. (Calculating q separately for each station and then av-

eraging does not substantially affect the outcome of this analysis.)

The probability of seeing the observed pattern of alleged failures of preservation over all the stations is the one-tailed, cumulative binomial probability of three or fewer successes out of 20 stations, where the probability of a success is $p = 0.3505$. This binomial probability is $P = 0.044$. We therefore reject the alternative hypothesis of preservational failure in favor of the null hypothesis. We interpret the existence of the three approximately contemporaneous layers as the coincidental result of local processes occurring within stations over distances of meters to tens of meters. This conclusion is supported by the fact that layers in the 270–380-yr range did not appear in cores extracted from stations closer to one or more of the three cores containing the layers than those three cores were to each other.

None of the remaining five anomalous layers (Table 2, Fig. 4) occurred in other cores from the same station or in cores from any other stations. Applying the same probability analysis to these singleton layers yields results that vary with sample size; the P value increases as the age of the layer increases, because the number of cores and stations sampled declines with increasing age. The probability that the 110-yr layer in core 97-12 represents a large-scale event is $P = 0.0005$, and for the 610-yr layer in core 99-15 the probability is $P = 0.025$. The probabilities associated with the three remaining singletons, from cores 99-9 (890 yr), 97-8 (1500 yr), and 00-1 (1670 yr), are $P = 0.10$, 0.45, and 0.54. Using Fisher's method of combining probabilities (a chi-square test; Sokal and Rohlf 1981), the alternative hypothesis can again be rejected ($\chi^2 = 30.01$, $df = 10$, $P < 0.001$). Like the three 270–380-yr layers, the five singleton layers represent localized events rather than the attenuated signals of larger scale episodes.

Another way to analyze this problem is to posit the alternative hypothesis that downslope transport due to processes at scales larger than the station but with variable effects at scales smaller than the study area (i.e., storms or tectonic events) removed substantial amounts of accumulating coral material, obscuring the fossil record of layers representing species turnover events. This explanation is unrealistic a priori, considering the protected location of the rhomboid shoals, the low angles of the paleoslopes sampled, and the orderly composition of the cores at all but two of the stations. If we estimate the loss due to downslope transport at an absurdly high 50% of reef accretion ($p = q = 0.5000$), the one-tailed, cumulative binomial probability of the putative large-scale layer remaining at three or fewer stations out of 20 is $P = 0.0013$. (Of course, we can arbitrarily raise the loss rate to 65% of reef accretion and obtain $P = 0.044$ as before.)

Perhaps a large-scale turnover event occurred, but it was completely lost from the record. The probability of an event not being preserved as a layer at any of

the 20 sampling stations is $0.50^{20} = 0.000001$ (one in a million). As discussed above, fewer stations were sampled at older ages. With only 10 stations available for consideration, the probability of an anomalous layer having been lost at all stations is $0.50^{10} = 0.001$ (one in a thousand). Thus, the second version of the alternative hypothesis can also be rejected at $P < 0.05$ in favor of the null hypothesis that the observed patterns resulted from localized events.

Finally, it is possible that system-wide hiatuses in reef growth occurred at times, due to population crashes of *Acropora cervicornis*. Such mass mortalities could not have been detected by our methods if the growth of *Acropora cervicornis* resumed rapidly enough that a layer of poorly preserved coral was not deposited. These cryptic hiatuses, if they occurred, are not equivalent to species turnover events and are not relevant to this analysis.

DISCUSSION

Disturbance and life history strategies

Reef communities living in the central Belizean lagoon are different now from the way they were during the rest of the late Holocene. *Acropora cervicornis* was the dominant coral for at least 3000 yr. High linear extension rates of *Acropora cervicornis*, combined with the propensity of this species to reproduce asexually by fragmentation (Shinn 1966, Gilmore and Hall 1976, Tunnicliffe 1981, Knowlton et al. 1990), ensured that the reefs were able to catch up to sea level, which was rising slowly during this period (Westphall 1986, Macintyre et al. 1995, 2000, Aronson et al. 1998).

The relatively unaltered *Acropora cervicornis* material in the cores suggested continuous burial in growth or near-growth position and rapid upward extension of the open framework of interlocking branches. During this period of rapid accumulation, *Acropora cervicornis* occasionally died over small areas and *Agaricia tenuifolia* recruited to the dead skeletons. In some cases the growth of *Acropora cervicornis* then resumed in the dead patches; in other cases *Agaricia tenuifolia* grew to dominate those small areas temporarily, before being overtopped by *Acropora cervicornis*.

White-band disease virtually eradicated *Acropora cervicornis* from the rhomboid shoals beginning in the late 1980s. Since *Acropora cervicornis* depends primarily on fragmentation to reproduce, its potential for recolonization was low once it had been removed (Knowlton 1992). High levels of herbivory allowed *Agaricia tenuifolia* to increase opportunistically and literally cover the entire study area for the first time in at least the last 3000 yr.

In less than a decade of dominance, *Agaricia tenuifolia* produced a layer of skeletal plates ~0.25 m thick. By the time the cores were extracted, the lower half of this *Agaricia* layer was already part of the Ho-

locene record, having been stabilized in sandy mud. Considering the rapid rate of burial, the high preservation potential of *Agaricia* in the central lagoon, and the fact that the paleoslopes sampled were less than the critical angle of repose for *Agaricia tenuifolia*, it is unlikely that an earlier, large-scale, *Acropora*-to-*Agaricia* replacement sequence would have gone unrecorded or undetected.

Agaricia tenuifolia possesses physiological and life history characteristics that favored its spread, by rapid growth and intensive local recruitment, once the incumbent populations of *Acropora cervicornis* had been removed by WBD. *Agaricia tenuifolia* tolerates the wide range of light and flow conditions experienced in the central lagoon (Helmuth et al. 1997a, b), and it grew rapidly there (Shyka and Sebens 2000). Caribbean agariciids reproduce by brooding internally fertilized planula larvae (Fadlallah 1983, Richmond and Hunter 1990, Richmond 1997), and *Agaricia tenuifolia* is no exception (Morse et al. 1988). Brooded lecithotrophic coral planulae have a flexible larval lifespan, enabling them to settle near their mother colonies (Fadlallah 1983, Harrison and Wallace 1990, Edinger and Risk 1995). The brooding coral species that have been studied, including *Porites astreoides* and *Agaricia agaricites*, are also hermaphroditic and self-fertilizing, enhancing reproduction at low colony densities in disturbed areas (Brazeau et al. 1998, Carlon 1999, Gleason et al. 2001). Brooding species, especially *P. astreoides* and *Agaricia agaricites*, are among the first corals to colonize disturbed reef surfaces in the Caribbean (Samarco 1985, Smith 1992, Edmunds 2000, and many others). If *Agaricia tenuifolia* is also hermaphroditic and self-fertilizing, that would help explain its ability to increase rapidly in the Belizean lagoon from initially low colony densities after the WBD outbreak had run its course.

Several months of high water temperatures in 1998, related in part to the El Niño–Southern Oscillation and possibly to global warming (Hansen et al. 1999, Karl et al. 2000), bleached and killed almost all *Agaricia tenuifolia* colonies in the central lagoon, leaving only a few small colonies and colony fragments alive. Since *Agaricia tenuifolia* had not dominated previously in the last several millennia, its loss due to bleaching was another novel event in the late Holocene history of the rhomboid shoals (Aronson et al. 2000). Whether the death of *Agaricia tenuifolia* and any subsequent replacement sequence will be preserved in the fossil record is a question for the future.

Rising sea level

Populations of the two *Acropora* species were killed and replaced by different coral species (and other taxa) during the Pleistocene deglaciations and in the Holocene, as reef accretion fell behind rapidly rising sea levels (reef drowning; replacement by deeper-dwelling species) and as inimical lagoonal and coastal waters

flooded fore-reef habitats (reef poisoning; replacement by more stress-tolerant species; Lighty 1981, Neumann and Macintyre 1985, Macintyre 1988, Fairbanks 1989, Blanchon and Shaw 1995). In other cases, populations of *Acropora* were able to catch up to and keep up with rising sea level in the Holocene. Relative sea level has risen only ~1 m over the last 3000 yr in the Caribbean (Lighty et al. 1982, Fairbanks 1989; Macintyre et al. 1995 and I. G. Macintyre, unpublished data, for Belize), which is slow relative to accretion rates measured for lagoonal *Acropora cervicornis* (Macintyre et al. 1977, Westphall 1986 for the rhomboid shoals).

That rising sea level did not cause sudden, widespread species turnover between *Acropora cervicornis* and *Agaricia tenuifolia* on the rhomboid shoals of Belize over the past three millennia is clear from the data presented in this paper. Furthermore, the recent transition to dominance by *Agaricia tenuifolia* cannot be attributed to rising sea level, considering (1) the fact that the shoals were keeping pace with sea level rather than lagging behind prior to the transition, and (2) the direct observation that white-band disease was the cause of mortality of the incumbent *Acropora cervicornis* populations (see Aronson and Precht 1997, Aronson et al. 1998). Nor was the transition a shallowing-upward effect of reef accretion; this explanation is negated by the broad depth range (3–15 m) of the transition to *Agaricia tenuifolia*. Shallowing-upward sequences on the rhomboid shoals involve the replacement of *Acropora cervicornis* by *Porites divaricata* and *Millepora alcicornis*, not *Agaricia tenuifolia* (Westphall 1986, Aronson et al. 1998, Macintyre et al. 2000).

Regional implications

In less than a decade, the scale of species turnover events in the central shelf lagoon of Belize increased from tens of square meters or less to hundreds of square kilometers or more. At approximately the same time *Acropora cervicornis* succumbed to white-band disease on the rhomboid shoals, *Acropora* spp. were killed en masse by WBD in back- and fore-reef habitats in Belize and throughout the Caribbean region (Aronson and Precht 2001a, b). Unlike the situation on the rhomboid shoals, however, herbivory on most reefs did not keep pace with coral mortality, leading to dramatic increases in the cover and biomass of macroalgae. These changes raise the possibility that the spatial scale of turnover on Caribbean reefs in general has increased.

Prior to the late 1970s, variation in the cover and composition of coral assemblages was generally high at small spatial scales, among quadrats within reef habitats (Jackson 1991). Kaufman (1977), for example, described small-scale patchiness in stands of *Acropora cervicornis* in Jamaica. This small-scale variability was brought about by the activities of damselfish (Pomacentridae), which killed *Acropora cervicornis* to cultivate algal lawns. Shinn et al. (1989) and Jaap and

Sargent (1994) noted short-term volatility in populations of *Acropora cervicornis* within reefs along the Florida Reef Tract during the 20th century. We suggest that the recent regional decline of *Acropora cervicornis* (and other corals) has eliminated much of this small-scale variation by limiting the scope for turnover events at small spatial and temporal scales.

The loss of *Acropora cervicornis* (as well as *Acropora palmata*), its limited prospects for rapid recovery in a small ocean basin now beset by disturbances and stresses, and the success of brooding corals as replacements (Sammarco 1985, Smith 1992, Connell 1997) lead us to concur with predictions that brooders, particularly in the families Poritidae and Agariciidae, will become increasingly dominant components of coral assemblages on Caribbean reefs (Kojis and Quinn 1994; Aronson and Precht 2001b). Regardless of their life history strategies, however, corals will not occupy the majority of space if severe disturbances and stresses continue at their present levels.

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